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Population dynamics of oribatid mites
(Acari, Cryptostigmata)
in an aspen woodland soil

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With 7 figures

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1. Introduction

A basic understanding of the population biology of oribatid mites is needed to assess their role in the soil since their population parameters will directly influence their interactions with both the abiotic and biotic components of this system. Although these mites are usually the most numerous forest soil arthropod (WALLWORK 1970), little is known about the population dynamics of individual genera or species. Most field studies on oribatids (e.g., VAN DER DRIFT 1951; EVANS, SHEALS and MACFARLANE 1961) have given much information on the seasonal fluctuations of the total mite community, while laboratory studies (LEBRUN 1970; SENGBUSCH and SENGBUSCH 1970) have indicated a wide range of developmental times (23 to 375 days) and indicate some of the inherent biological variability within the oribatids. This variability has also been established in the few studies which have examined the population biology of individual oribatid species (e.g. JALIL 1965; LEBRUN 1969; BÄUMLER 1970).

The present study was initiated to compare the population biology of individual oribatid species utilizing both laboratory and field data. This work was the first to present population data on Canadian oribatids and the first to present a life table analysis of an oribatid mite. Information on horizontal and vertical distribution, feeding, and energetics has been given previously (MITCHELL 1974, 1975; MITCHELL and PARKINSON 1976).

2. Site, taxa and methods

2.1. Site description

The study area was in the Kananaskis Valley of Alberta, Canada (51°02' N, 105°01' W; 1400 m elevation). The dominant overstory vegetation was composed of aspen (*Populus tremuloides* MICHX.) and balsam poplar (*P. balsamifera* L.). The ground flora of woody perennials, forbs, and grasses was well developed. The soil was an Orthic Gray Luvisol with distinct litter (L), fermentation (F), and humus (H) horizons (KARKANIS 1972).

Soil temperature data were collected at 3 depths with a distance thermograph (Figure 1). The L, F, and H horizons generally remained frozen and snow covered from November to March while during summer, soil temperature increased reaching a maximum in late July or early August. Temperature data were converted into degree-weeks and summarized (Table 1). Soil moisture remained high and constant during the winter and decreased to a minimum during periods of highest temperature. For more details MITCHELL (1974) should be consulted.

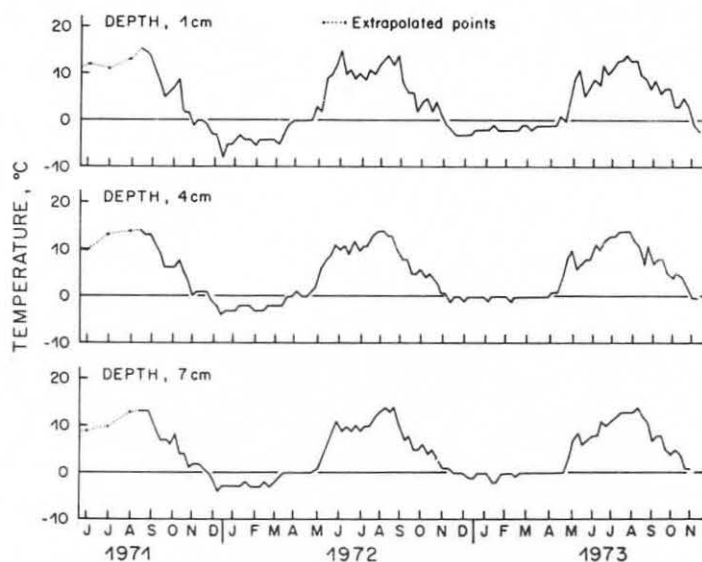


Fig. 1. Temperature of L (1 cm), F (4 cm) and H (7 cm) horizons in aspen woodland soil.

Table 1. Aspen woodland, soil temperature summary (November 1, 1971 — November 1, 1973)

Depth cm	Mean °C	Maximum °C	Minimum °C	Degree-weeks above zero	
				°C 1972	°C 1973
1	3.3	41	-11	221.4	219.6
4	4.2	18	-4	232.4	225.6
7	3.9	16	-4	218.6	230.4

Table 2. Oribatid taxa studied

Family	Taxon	Adult length μm (10^{-6})
Ceratozetidae	<i>Ceratozetes kananaskis</i> MITCHELL	402
Ceratozetidae	<i>Ceratozetes gracilis</i> (MICHAEL)	550
Oribatulidae	<i>Scheloribates</i> ssp.	400
Eremaeidae	<i>Eremaeus foveolatus</i> HAMMER	540
	<i>Eremaeus</i> sp. B.	
Cepheidae	<i>Euplerotegaeus rostratus</i> HIGGINS et WOOLLEY	612

2.2. Taxa studied

Within the study area 30 oribatid taxa were distinguished of which 5, based on abundance and relative large size, were chosen for population study (Table 2). Data for *Eremaeus foveolatus* Hammer and *Eremaeus* sp. B were pooled since the immatures of these species could not be readily distinguished. Similarly all *Scheloribates* ssp. were grouped together because adults could not be easily separated.

Euplerotegaeus rostratus and *Eremaeus* ssp. were most common in the L horizon, while *Ceratozetes kananaskis*, *C. gracilis*, and *Scheloribates* ssp. were most abundant in the F and H horizons (MITCHELL 1974). In the field all developmental stages (adult, nymphs, larva) were studied for *C. kananaskis*, *C. gracilis* and *Eremaeus* ssp. while only adults were studied for *Scheloribates* ssp. and *E. rostratus*.

2.3. Sampling

Three subplots (3 m × 3 m) were laid out in an area with no marked differences in herbaceous vegetation and a minimal slope gradient. Soil cores (surface area of 22.9 cm²) were taken to a depth of 10 cm and subdivided into 4 equal depths. This depth generally included all organic horizons (L, F, H) and the vast majority of soil arthropods. At each sampling period 3 random cores were taken from each subplot for a total of 9 samples and 36 subsamples. Sampling was carried out from May 1971 through May 1973, biweekly when the soil was above 0 °C and every fourth week when frozen. One additional sample was taken on 9. April 1971 at a nearby (50 m) location within the aspen stand.

2.4. Extraction and counting

Based on the studies of MACFADYEN (1961), BLOCK (1966b), and PANDE and BERTHET (1973) the high gradient extractor was chosen as being best suited for population studies of non-phthiracarid oribatids in woodland soil where many samples and individuals must be analyzed, although extraction efficiency limitations may decrease the accuracy of population estimates. All extractable mites were collected over 5 days with a gradual increase of temperature to 70 °C at the sample surfaces.

After extraction into water, animals were killed in 95% ethanol, concentrated in a Millipore-filter apparatus, and cleared in lactic acid. Counting was done with a stereomicroscope and the designated taxa separated into larvae, nymphs and adults. (Only adults of *Scheloribates* spp. and *E. rostratus* were counted.) For each sampling time up to 30 adults and 40 immatures of each taxon were slide-mounted in Hoyer's medium using randomly selected specimens. Mounts were examined using a phase contrast microscope for the following: sex of adult (determined by presence or absence of an ovipositor), number of eggs and stage (larva, protonymph, deutonymph, tritonymph). All arthropods were separated into higher taxonomic categories from the 9. April 1971 sample.

2.5. Population estimates and stage duration

Estimates of the adult, total nymphal and larval populations were obtained directly from the counted samples. The fraction of each nymphal stage was determined from the permanent mount subsamples and then multiplied by the total nymphal population to give density. Egg data were derived from adult subsamples in which the mean number of eggs/adult was multiplied by adult density. To normalize the frequency distribution of samples, a logarithmic transformation was employed (GERARD and BERTHET 1966; MITCHELL 1974) and results were expressed on a m² basis with arithmetic means and 95% confidence limits. For those estimates derived from subsampling only means were given.

2.6. Life stage duration

Two methods were utilized to determine the life stage duration. (1) Laboratory cultures with a plaster of Paris and charcoal substrate were kept at 15 °C. Adult animals were introduced into the cultures along with fungal food sources. Cultures were examined weekly and the number of immatures and their stages noted (MITCHELL and PARKINSON 1976). (2) The field population data were examined for peaks between successive stages using the time between population peaks of stages to estimate field life stage duration.

3. Results and discussion

3.1. Density and phenology

In a comparison of total arthropod densities the Acari constituted greater than 50% of the total soil arthropod community with the Acari order Cryptostigmata (Oribatei) being by far the most numerous (Table 3). The absolute and relative densities of these taxonomic groups were similar to those findings in other moder and mor temperate woodland soils (e. g. EVANS et al. 1961; WALLWORK 1970).

Table 3. Arthropod densities in aspen woodland soil, 9. April 1971

Category	10 ³ m ² (± 95 % confidence limits)*)	% of total arthropods
Cryptostigmata	122.9 ± 79.9	44
Prostigmata and Astigmata	25.3 ± 34.4	9
Mesostigmata	7.4 ± 9.2	3
Collembola	71.4 ± 125.9	26
Total Acari	158.3 ± 119.6	57
Total Arthropods	278.2 ± 245.8	100

*) Multiply values in column by 10³ to obtain density per m².

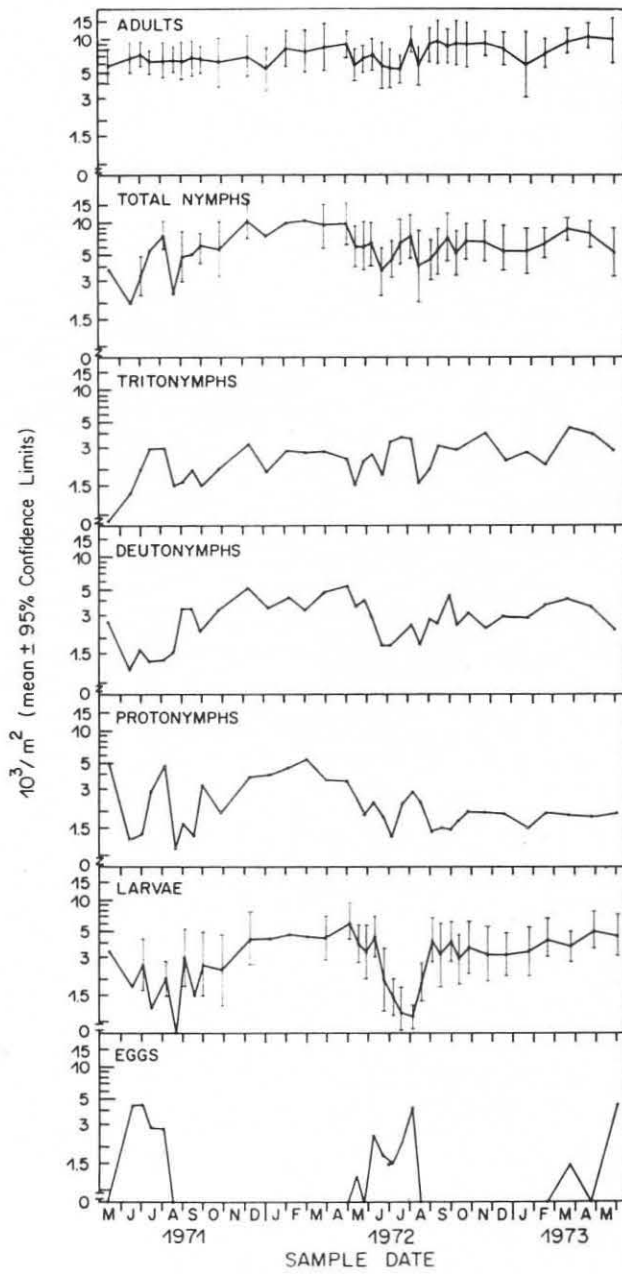


Fig. 2. *Ceralozetes kananaskis* population densities, estimated from 9 samples per time interval. Multiply by 10^3 for density per m^2 .

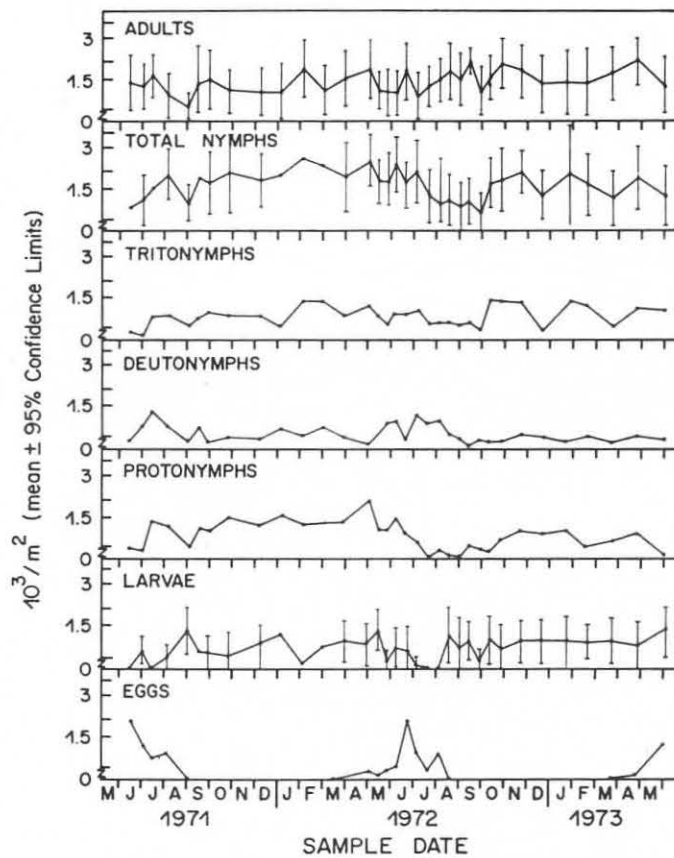


Fig. 3. *Ceratozetes gracilis* population densities, estimated from 9 samples per time interval. Multiply by 10^3 for density per m^2 .

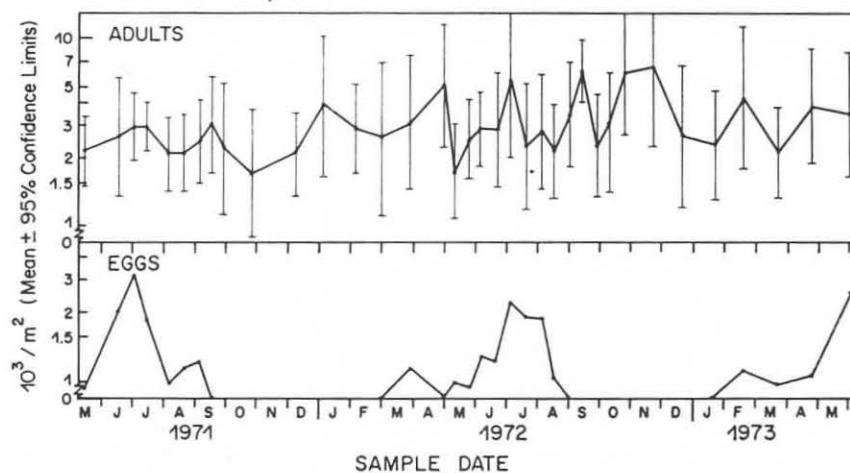


Fig. 4. *Schelorbates* ssp. population densities, estimated from 9 samples per time interval. Multiply by 10^3 for density per m^2 .

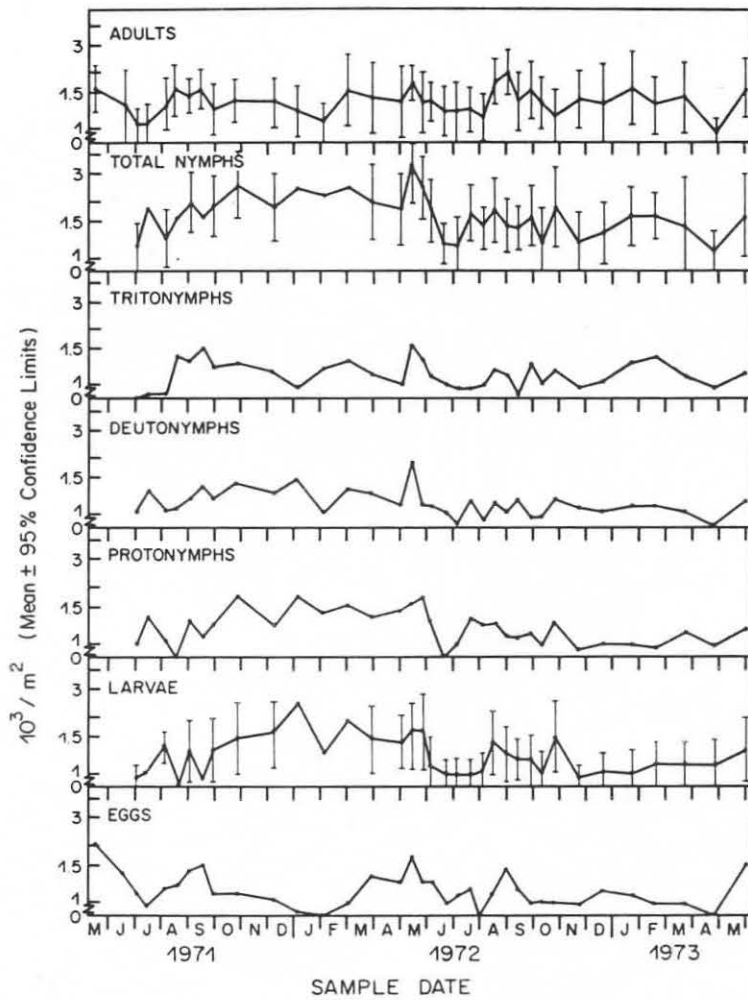


Fig. 5. *Eremaeus* ssp. population densities, estimated from 9 samples per time interval. Multiply by 10³ for density per m².

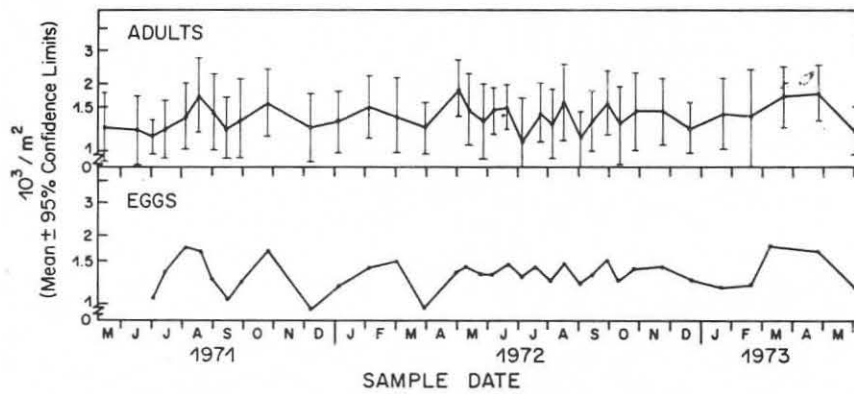


Fig. 6. *Eupterotegaeus rostratus* population densities, estimated from 9 samples per time interval. Multiply by 10³ for density per m².

The seasonal population densities of the five intensively studied taxa were presented graphically (Figures 2—6) and their means summarized (Table 4). Phenology was determined from density variations of stages based on abrupt changes in densities and peak synchrony between years. Although peak definition and synchrony were not definitive the following interpretations were put forth for discussion purposes and to allow derivation of testable hypotheses.

Ceratozetes ssp. (Figures 2 and 3) and *Scheloribates* ssp. (Figure 4) showed a circumscribed egg production period beginning in early spring, peaking in June or July, and dropping off rapidly in early August. Initiation of egg maturation coincided with decreasing moisture and increasing temperature (Figure 1). Moreover, in both *Ceratozetes* ssp. larvae which must have developed from the eggs laid earlier in the summer increased during August.

For only *C. kananaskis* can peaks in nymphal stages be observed. The protonymphs became more abundant in July, deutonymphs in late August (1971) or September (1972), and tritonymphs in July. It can be hypothesized that for *C. kananaskis*, eggs are laid in mid-summer with development up to larvae and/or protonymphs occurring into late summer and autumn. The following spring deutonymphs appear with tritonymphs developing in late summer. Next summer, the tritonymphs develop into adults which overwinter and lay eggs the subsequent summer. The total life cycle would take about 3 years. Overwintering occurred in all stages of both *Ceratozetes* ssp. with the probable exception of the egg.

Table 4. Mean Oribatid population density of all sample dates

Taxa	10 ³ /m ² ± 95 % confidence limits*) (number of samples)		
	Adult	Nymph	Larva
<i>Ceratozetes kananaskis</i>	6.61 ± 0.53 (36)	5.29 ± 0.72 (36)	2.36 ± 0.46 (36)
<i>Ceratozetes gracilis</i>	0.57 ± 0.08 (34)	0.72 ± 0.11 (34)	0.24 ± 0.05 (34)
<i>Scheloribates</i> ssp.	2.21 ± 0.42 (36)	—	—
<i>Eremaeus</i> ssp.	0.47 ± 0.07 (36)	0.81 ± 0.17 (34)	0.38 ± 0.11 (34)
<i>Eupterolegaeus rostratus</i>	0.52 ± 0.07 (36)	—	—

*) Multiply values in column by 10³ to obtain density per m².

No data collected (—).

Table 5. Coefficient of variation*) of population density during growing season

Taxa	Developmental stage				
	Larva	Proto-nymph	Deuto-nymph	Trito-nymph	Adult
<i>Ceratozetes kananaskis</i>	69	71	59	53	25
<i>Ceratozetes gracilis</i>	75	87	76	47	44
<i>Eremaeus</i> spp.	68	70	81	77	47

*) Coefficient of variation = (Standard deviation × 100)/Mean.

Table 6. Sex ratio — Chi-square test for 1:1 fit

Category	<i>Ceratozetes kananaskis</i>	<i>Ceratozetes gracilis</i>	<i>Scheloribates</i> ssp.	<i>Eremaeus</i> ssp.	<i>Eupterolegaeus rostratus</i>
Females	450	270	456	204	167
Males	550	228	470	206	199
Females/Male	.82	1.18	.97	.99	.84
Chi-Square (χ^2)	10.00	3.54	.21	.01	2.80
P*)	<.01	.28	.65	.92	.09

*) P = probability that χ^2 will be exceeded.

In New York HARTENSTEIN (1962) found in *C. gracilis* that eggs were deposited in the spring and summer. September and October samples had many larvae and protonymphs while in November only deutonymphs, tritonymphs and adults were found. March and May samples contained only tritonymphs and adults.

For *Eremaeus* ssp. and *Eupterotegeaeus rostratus* (Figures 5 and 6) there were no synchronous peaks in egg production. Egg laying may have occurred throughout the growing season during favourable conditions.

Coefficients of variation of population density of three taxa, for the growing season (May to November), were determined (Table 5). For both *Ceratozetes* ssp. there was a trend for decreasing variation with age. For *Eremaeus* ssp. no marked decrease occurred until the adult stage. These decreases can be attributed to a greater overlap of generations and increasing variation in development rate with age (LEBRUN 1970).

Sex ratios were determined by pooling all adult specimens collected in subsampling and tested for a 1:1 relationship (Table 6). For only *C. kananaskis* was this hypothesis rejected ($P < .05$) with this species having a higher proportion of males.

3.2. Temperature and life stage duration

In order to compare culture and field data, the effect of temperature on developmental rate must be considered. Because of its simplicity and applicability, a degree time formulation, in which development is linearly related to temperature (BLUNCK 1923), was applied to the present study assuming a developmental threshold at 0 °C. Degree-weeks for the field data were calculated by a summation of the mean weekly temperature between successive developmental stages. The 4 cm depth temperature was used for *Ceratozetes* ssp. since this was the depth of greatest abundance (MITCHELL 1974). The degree-weeks for development of *C. kananaskis* were determined by utilizing phenology data and assuming the following development times: (1) egg-larva, July 1971—Aug. 1971; July 1972—Aug. 1972; (2) larva-protonymph, Aug. 1971—July 1972; (3) protonymph-deutonymph, July 1971—Sept. 1971; July 1972—Sept. 1972; (4) deutonymph-tritonymph, Sept. 1971—July 1972. If two estimates were available, these results were averaged. Since no peaks of adult recruitment were evident, no estimate of field developmental time from tritonymph to adult was possible. For laboratory data, development time in weeks was multiplied by the rearing temperature of 15 °C.

There was a good correspondence between field and laboratory data for *C. kananaskis* (Table 7). Also HARTENSTEIN's (1962) laboratory rearing data for *C. gracilis* were converted to degree-weeks and were markedly different from the present findings; the differences could be explained by intraspecific differences and/or a lack of fit for the degree-time relationship.

Table 7. Developmental time in degree-weeks for *Ceratozetes* spp.

Species Condition	<i>Ceratozetes kananaskis</i>		<i>Ceratozetes gracilis</i>	
	Laboratory culture 15 °C	Field data	Laboratory culture 15 °C	Laboratory culture 20 °C (HARTENSTEIN, 1962)
Stage				
egg-larva	60	67	60	91
larva-protonymph	75	78	75	57
protonymph-deutonymph	75	84	75	102
deutonymph-tritonymph	90	98	90	80
tritonymph-adult	165	no data	240	54
Total	465	—	540	340—426*)

*) Range of total developmental time.

When the total developmental time was divided into the mean number of degree-weeks in a year (Table 1), field developmental times of 2.1 and 2.4 years were found for *C. kananaskis* and *C. gracilis* respectively. These results agree with the phenological observations for *C. kananaskis*. It should be emphasized that this field developmental time could differ considerably for a given individual. These developmental times are longer than those predicted by other workers. For *C. gracilis* HARTENSTEIN (1962) postulated a one-year life cycle in warmer New York and HAARLØV (1960) found a developmental time of 41 days for *C. gracilis* at 20 °C.

WOODRING and COOK (1962) have given the only other field generation times for the genera being considered. They postulated, using laboratory data, that *Scheloribates laevigatus* and *Ceratozetes cisalpinzi* would have 3 and 4–5 generations per year in Minnesota. There has been a tendency in oribatid mite population studies to generalize from laboratory developmental times to those in the field without the necessary field data. This form of extrapolation is very tenuous since most laboratory rearings have been carried out at temperatures (20 °C or higher) which are greater than those usually encountered in temperate forest soils.

3.3. Life table for *C. kananaskis*

Three difficulties attended the formidable task of estimating survivorship of *C. kananaskis* in the field: (1) Developmental time depended on various environmental parameters (e.g., temperature). (2) Developmental times varied between individuals. (3) Overlapping generations were present. Nevertheless an attempt has been made to produce a life table for this species.

For estimating the number of animals present in any given stage, the following model can be applied where:

$$S_{a+1} = \sum_0^t (n_{aTt}/D_a) - M_a \quad (1)$$

where

t = total time in weeks,

S_{a+1} = total number of animals entering stage ($a + 1$),

n_{aTt} = number of animals in stage (a) at time (t) multiplied by the temperature (T),

D_a = duration of stage (a) to ($a + 1$) in degree-weeks, and

M_a = mortality in stage (a).

The model expresses animal numbers by their physiological age (degree-weeks) to account for temperature effects on development. A similar physiological age formulation has been used by HUGHES (1963) for aphid populations. In the present model, animals were lost from a stage in two ways, either by developing into the next stage or by mortality. It was assumed that emigration and immigration were at an equilibrium within the sampling area; few oribatids were found in above ground vegetation. Other inherent assumptions were that development time in degree-weeks remained constant at all temperatures and that each year contributed an equal number of individuals to each stage since more than one generation may be represented in any given sample. Field population data for *C. kananaskis* (Figure 5) were combined with the temperature data from the 4 cm depth to determine n_{aTt} for each stage and developmental times (D_a) were taken from the laboratory rearing experiments (Table 7). Field data for the two years were incorporated with weekly summation and extrapolation where necessary.

Because some data needed for the model were not available, other estimates and assumptions were employed:

(1) Since mortality could not be assessed directly, it was assumed that it occurred at the termination of each stage so that the following would hold:

$$S_a = n_{aTt}/D_a. \quad (2)$$

Mortality was expressed as a percentage of the previous stage:

$$\text{percent mortality stage (a)} = \frac{S_a - S_{a+1}}{S_a} \times 100. \quad (3)$$

This assumption becomes less valid as mortality is shifted toward the beginning of the stage, which would decrease the estimate of S_a . The method of RICHARD, WALOFF and SPRADBERY (1960) which assumes constant mortality, could not be used since my data lacked the necessary precision.

(2) Although there was no measurement of adult life span in the field, it was noted in the laboratory that they would live for over 12 months which corresponds to over three years of field temperatures. BLOCK (1965) found adult longevity in the laboratory of *Platynothrus peltifer* and *Damaeus clavipes* to be equal to or greater than one year at 5 °C. WOODRING and COOK (1962) recorded at 25 °C an adult life span of 10–12 months for *Ceratozetes cisalpinus*. Thus a life span of three years was used where:

$$S_a = n_{AT}/D_a \text{ and } D_a = 684 \text{ degree-weeks.}$$

(3) There was no measurement of fecundity so it was assumed that the females laid the maximum number of eggs (3) observed within them and that these were laid in one batch. WOODRING and COOK (1962) found that *C. cisalpinus* laid all eggs in one batch. It was also assumed that the sex ratio of eggs was 1 to 1 which fits the adult data fairly closely (Table 6).

The calculations derived from the model were summarized (Table 8). Because of various assumptions, these data must be interpreted with caution, but they do indicate a trend for increasing mortality throughout the animal's life cycle when expressed in physiological time. The negative mortality for the protonymph was probably a reflection of inaccurate sampling and/or model assumptions. These results were also shown as a survivorship curve in which both the actual model curve and the smoothed curve showed a resemblance to the Type IV curve (SLOBODKIN 1961) in which mortality decreases with age (Figure 7). It has been suggested that the soft-bodied immatures of oribatids are more susceptible to predation (MADGE 1964) and to desiccation (JALIL 1972) than hard-bodied adults which may account for the higher juvenile mortality.

Although the precise assessment of mortality factors in *Ceratozetes kananaskis* would be beyond the accuracy and scope of this work, it was noted that egg laying occurred in the driest and warmest period of the year in *C. kananaskis*. BÄUMLER (1970) found a similar egg laying pattern for *H. gibba* which he attributed to the egg stage's ability to utilize warm temperatures while larvae which were not resistant to desiccation and high temperatures were least numerous at this period. In the present study there was no evidence that freezing caused marked mortality since winter samples did not show decreasing numbers with decreasing temperatures; similar findings were reported by SENGBUSCH (1951) and REEVES (1969). Biological components of mortality were not documented but BÄUMLER (1970) has found that a gregarine parasite affected the population dynamics of *H. gibba*.

A life and fertility table (SOUTHWOOD 1966) was constructed for *Ceratozetes kananaskis* (Table 9). The pivotal age in degree-weeks (x) was given as the median age of each stage. As previously designated the survivors (l_x) remained constant in a given stage. Also since eggs were laid in single yearly batches, it was necessary to estimate the age specific fertility (m_x) for only one time for a given year. For brevity, the adult population survivors (l_x) were only given for two times a year since the adult survivors remained constant in the model.

Table 8. Summary of model calculations for survivorship of *Ceratozetes kananaskis*

Stage	Number entering stage S_a animals/m ² /year	Physiological time mortality M_a/D_a animals/degree-week of development	Percent mortality $\frac{S_a - S_{a+1}}{S_a} \cdot 100$
egg	8915	62.4	42
larva	5169	20.8	30
protonymph	3610	-2.0	-4
deutonymph	3760	14.0	50
tritonymph	2500	2.2	15
adults	2133	3.1	100

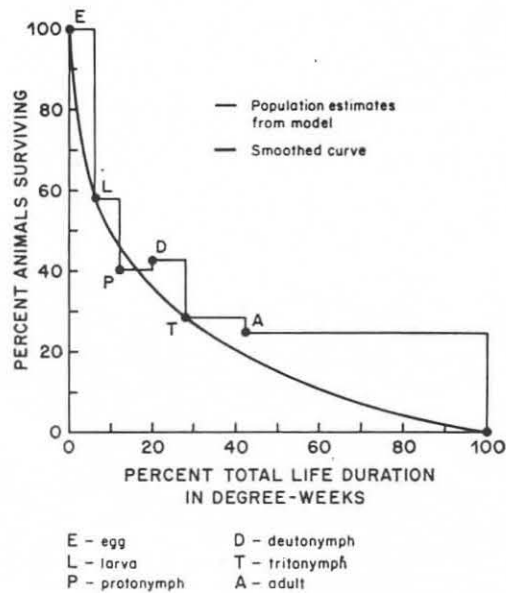


Fig. 7. Survivorship curve of *Ceratozetes kananaskis*.

The net reproductive rate (R_0) of *Ceratozetes kananaskis* would be expected to be near 1.0 since the adult population density remained relatively constant (Figure 2). The calculated R_0 value of 1.076 was quite close to this predicted value. The stable population was also reflected in the small capacity of increase (r_c) of .000077/degree-weeks. The long mean generation time (T_c) of 4.2 years again emphasizes the importance of the long life cycle and low fecundity in determining population parameters. In addition, although mortality was concentrated in the immature stages, still 24% of the eggs reached the adult stage. This percentage must be considered high when compared to other terrestrial arthropods such as the winter moth in which only 0.7% of the eggs survived (VARLEY, GRADWELL and HASSELL 1973).

Table 9. Life and fertility table for *Ceratozetes kananaskis*

Stage	x degree-weeks	l_x	m_x
egg	34	1.000	0
larva	106	.579	0
protonymph	187	.404	0
deutonymph	287	.421	0
tritonymph	410	.280	0
adult (late summer)	492	.239	0
adult (winter)	607	.239	0
adult (early summer)	721	.239	1.5
adult (winter)	836	.239	0
adult (early summer)	950	.239	1.5
adult (winter)	1064	.239	0
adult (early summer)	1179	.239	1.5
adult (winter)	1293	.000	0

$$R_0 = \sum l_x m_x = 1.076$$

$$\sum l_x m_x x = 1021.7$$

$$T_c = \frac{\sum l_x m_x x}{R_0} = 949.6 \text{ degree-weeks} = 4.2 \text{ years}$$

$$r_c = \frac{\log_e R_0}{T_c} = .000077/\text{degree-weeks}$$

In the only other study of population structure in an oribatid, LEBRUN (1969) using *Nothrus palustris* constructed age pyramids from which comparisons between seasons and stages were derived; he gave no estimate of fecundity. Of the active stages, the larvae and protonymphs suffered the greatest mortality which agrees with the present findings. Also the total population numbers of *N. palustris* did not fluctuate markedly between seasons during his one-year study, which again coincide with the results for *C. kananaskis*.

4. Population biology of oribatids and their role in the soil

Ceratozetes kananaskis, *C. gracilis* and *Scheloriobates* ssp., which inhabited the F and H horizons, showed a remarkable synchrony in the initiation and termination of egg maturation. On the other hand, *Eremaeus* ssp. and *E. rostratus*, which were found in the L horizon, showed no seasonal egg maturation pattern. This dichotomy in the biology of the L versus the F—H inhabitants was also evident in their distributional patterns (MITCHELL 1974) and feeding biology (MITCHELL and PARKINSON 1976). Seasonal egg maturation has been found in *Platynothrus peltifer* (HARDING 1973), *Humerobates rostromellatus* (MURPHY and BALLA 1973), and *N. silvestris* (WEBB 1970). In *Rhysotritia duplicata* (HARDING 1969) and *N. palustris* (LEBRUN 1970) eggs were always present.

Little information has been gathered on the physical and biological factors affecting the phenological patterns of oribatid mite populations, although there are major differences in life cycle durations between species (LEBRUN 1971). In the present study, entry to the larval stage of the *Ceratozetes* ssp. was seen to coincide with increasing soil moisture. In the same period food resources in the form of fungal hyphae may also have been increasing as indicated by gut content analysis (MITCHELL and PARKINSON 1976). Thus the larvae were being produced at the most opportune time.

It has been speculated that the spring and autumn may be periods of high reproductive activity owing to favourable moisture conditions with bimodal peaks in oribatid density being found by many European workers at these times (e.g., FORD 1937, 1938; HAARLØV 1969; EVANS et al. 1961; BLOCK 1966a). However, it has been difficult to interpret the underlying causes of these population fluctuations. Unless the actual recruitment pattern has been examined, the interpretation of seasonal density fluctuations gives little concrete information on the biology of this group. This problem becomes even more important when the total oribatid community is examined since variation of recruitment and life cycles between species cannot be ascertained. In addition, sampling may be biased by changes in extraction efficiency with developmental stage and season.

However, there has been some information indicating that recruitment may be affected by similar physical conditions in different study areas. For instance in New York, REEVES (1964) found highest larval densities for *Tectocepheus velatus*, *Oppia nova*, *O. subpectinata*, *Pergalumna altera* and *Oribatella* sp. in a period (June—August) following low soil moisture; a similar pattern for *H. gibba* was found by BÄUMLER (1970) in West Germany. This same pattern of larval development was seen for the two *Ceratozetes* ssp. and, judging by the egg phenology, it was also present for *Scheloriobates* spp. In Michigan, WALLWORK (1959) found in the field many eggs during the summer, with a decrease caused by hatching taking place through late summer and autumn.

Long life cycles of the oribatids have important implications concerning their role in soil. With such a protracted period of development these animals would not be able to numerically respond to sudden changes in resources or mortality rates. Other more rapidly reproducing soil organisms would not have these limitations. For instance, within the same aspen site LOUSIER (1974) has shown a generation time of 6.8 days for Testacea (Rhizopoda) contrasted to the generation time of 4.2 years for *C. kananaskis*. Populations with these short generation times (r-strategists) would be expected to feed on labile organic substrates or organisms with short generation times (e.g., bacteria) and exhibit the most marked density fluctuations; while in contrast, populations with long generation times (K-strategists) would be expected to consume non-labile substrates or organisms with relatively long gene-

ration times (e. g., Basidiomycete fungi) and also exhibit lower density fluctuations. Since the life cycles of the various component species within a taxonomic grouping, varies greatly, there is an opportunity for developing various life history strategies adapted to the mosaic of the soil's physical environment and food resources (MITCHELL and PARKINSON in press).

Also the oribatids examined in the present study exhibited iteroparity (repeated reproduction) as indicated in the life table analysis for *C. kananaskis*. COLE (1954) suggested that iteroparity would be most advantageous in terms of maximizing the intrinsic rate of increase (r_m) in species with uncertain survival or pre-reproductives and relative stable survival of the reproductives. This stability of reproductives was indicated for all five taxa in the present study. Moreover, the higher mortality in immature *C. kananaskis* showed the possibility for uncertain survival in the early stages. MURPHY (1968) stated that the stability of tropical faunas might be a consequence of their relatively long lives and low birth rates in conjunction with iteroparity. An analogous situation may be seen in the oribatid soil community which exhibits low numerical density fluctuations and a high species diversity.

An examination of the population parameters gives needed information on the basic biology of oribatids and gives insight into their functional interrelationships within the soil. To further the understanding of their role, the population biology of more species must be examined in a variety of soil environments emphasizing an analysis of field life cycles and a determination of how these life cycles are affected by the biological and physical environment of the soil.

5. Summary · Zusammenfassung

(1) The population biology of 5 oribatid mite taxa from an aspen woodland soil was examined. *Ceratozetes kananaskis*, *C. gracilis* and *Scheloriabates* ssp. were predominant in the fermentation layer (F) and humus (H) while *Eremaeus* ssp. and *Eupterotegeus rostratus* were restricted to the litter (L) horizon.

(2) The population densities of all developmental stages (egg, larva, protonymph, deutonymph, tritonymph and adult) of *C. kananaskis*, *C. gracilis* and *Eremaeus* ssp. were estimated from May 1971 to May 1973 by random core sampling and high gradient extraction. For *Scheloriabates* ssp. and *E. rostratus* only the densities of eggs and adults were determined. The phenology of developmental stages showed a spring-summer egg maturation period for the three F-H inhabitants while L adults contained eggs throughout the year.

(3) The developmental times of *C. kananaskis* and *C. gracilis* were determined by laboratory cultures and in the former species were compared to field developmental times based on physiological time (degree-weeks). For *C. kananaskis* the laboratory and field data showed good correspondence and indicated a developmental time of 465 degree-weeks or 2.1 years in the field.

(4) A population model for estimating the number of individuals entering a given developmental stage was presented and applied to the field population of *C. kananaskis*. Calculations were summarized in a survivorship curve and life table, which indicated that mortality rate was greatest in the early developmental stages. Generation time (T_c) and capacity of increase (r_c) were calculated to be 4.2 years and .00008/degree-weeks, respectively, which reflects the slow rate of development and stable population structure.

(5) The relationship of oribatid mite population biology to their functional role in the soil was discussed.

Populationsdynamik von Oribatiden in einem Espenwald

(1) Populationen von fünf Oribatidenarten wurden biologisch, insbesondere bionomisch untersucht. *Ceratozetes kananaskis*, *C. gracilis* und *Scheloriabates* ssp. waren in der Fermentationsschicht (F) und im Humus (H) prädominant, während *Eremaeus* ssp. und *Eupterotegeus rostratus* auf die Streuschicht (L) beschränkt waren.

(2) Die Populationsdichten aller Entwicklungsstadien (Eier, Larven, Proto-, Deuto- und Tritonymphen sowie Adulte) von *C. kananaskis*, *C. gracilis* und *Eremaeus* ssp. wurden von Mai 1971 bis Mai 1973 auf Grund von zufälligen Probenentnahmen (mit Bodenbohrer) und „high-gradient-extraction“ der Bodentiere geschätzt. Für *Scheloriabates* ssp. und *E. rostratus* wurden lediglich die Anzahl (densities) der Eier und Adulten bestimmt. Die Phänologie der Entwicklungsstadien zeigte eine Frühjahrs-Sommer-Periode der Eireifung für die drei den F- und H-Horizont bewohnenden Arten, während der L-Horizont das ganze Jahr über Eier enthielt.

(3) Die Entwicklungsdauer von *C. kananaskis* und *C. gracilis* wurde durch Laboratoriumskulturen bestimmt und bei den vorgenannten Arten wurde sie mit der Entwicklungsdauer im Freiland verglichen und auf physiologische Zeit umgerechnet (Temperatursummen-Wochen bzw. „degree-

weeks"). Bei *C. kananaskis* zeigten die Laboratoriums- und Freiland-Daten eine gute Übereinstimmung und ergaben eine Entwicklungsdauer von 2,1 Jahren im Freiland oder eine Summe von wöchentlichen Durchschnittstemperaturen von 465 °C.

(4) Ein Populations-Modell zur Schätzung der Anzahl der Individuen, die ein bestimmtes Entwicklungsstadium beginnen, wurde vorgestellt und auf den Freilandbesatz von *C. kananaskis* angewandt. Die Schätzwerte wurden in einer Überlebens-Kurve und in einer Lebensstafel (life table) zusammengefaßt, die zeigt, daß die Mortalitätsrate in den ersten Entwicklungsstadien am größten war. Die Generationsdauer (T_c) und die Vermehrungskapazität (r_c) wurden auf 4,2 Jahre bzw. .00008/Temperatursummen-Woche geschätzt; dies zeigt die langsame Entwicklungsdauer und die stabile Populationsstruktur.

(5) Die Beziehung zwischen der Lebensweise der Oribatiden-Populationen und ihrer funktionellen Rolle im Boden wurde diskutiert.

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